Intra-tree foraging behavior of *Ceratitis capitata* flies in relation to host fruit density and quality

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Abstract

We examined the intra-tree foraging behavior of individually-released, wild-population Mediterranean fruit flies (medflies), *Ceratitis capitata* (Wiedemann), on field-caged host trees bearing each of three different densities (0, 3, or 12 per tree) of non-infested host fruit (kumquat) or each of two levels of fruit quality (12 non-infested fruit or 12 fruit infested with eggs and covered with host marking pheromone). With increasing density of non-infested fruit, medflies tended to remain longer in trees, visit more fruit before leaving, oviposit more often, accept a proportionately smaller number of fruit visited, and emigrate sooner after the last egg was laid (i.e. have a shorter Giving-Up-Time). Medflies spent much less time, oviposited much less often, and exhibited a longer Giving-Up-Time on trees harboring pheromone-marked fruit than non-infested fruit. Variation in temperature within the range at which experiments were conducted (25–36 °C) had little detectable influence on foraging behavior. We compare our findings with published findings on the intra-tree foraging behavior of another tephritid fly, *Rhagoletis pomonella* (Walsh), and with current foraging behavior theory. We discuss implications of our findings with respect to medfly management strategies, particularly fruit stripping in eradication programs and use of synthetic marking pheromone for control.

Introduction

An oft-repeated axiom of integrated pest management is that detailed knowledge of the behavior and ecology of the target pest is required for effective control. Specifically, what is needed is analysis of the insect's behavior under conditions appropriate to integrated pest management practices.

Among true fruit flies, two management practices directly rooted in fly behavior have been proposed or put into practice. First, the stripping of fruit from already-infested or potentially infestable host plants is a common practice in many fruit fly eradication or population suppression programs (Jackson &

Lee, 1985; Anonymous, 1986). Second, application of synthetic host marking pheromone has been proposed as a means of fly management through deterrence of oviposition in fruit (Prokopy, 1972; Boller, 1981). In the first practice, fruit density is manipulated. In the second, fruit quality is manipulated. Although considerable information is available on certain aspects of host-selection behavior in several tephritid species (see Prokopy, 1983; Prokopy & Roitberg, 1984 for reviews), the effect of host fruit density and quality on fly foraging behavior under relatively natural conditions is not well understood for most species.

Until now, quantitative analysis of tephritid fly

foraging behavior, involving detailed tracking of the movement of individuals over time and over a range of fruit density and quality conditions, has been carried out almost exclusively in the apple maggot fly, *Rhagoletis pomonella*. The results (Roitberg *et al.*, 1982; Roitberg & Prokopy, 1984; Prokopy & Roitberg, 1984, 1987) reveal mature *R. pomonella* females (a) emigrate within a few minutes after release on small host trees devoid of fruit; (b) discover (visit) more fruit, oviposit more often, and remain longer in host trees that harbor higher densities of non-infested host fruit than lower densities of non-infested host fruit or higher densities of pheromone-marked infested host fruits; (c) accept a proportionately smaller number of fruit visited as density of non-infested host fruit increases; and (d) exhibit a decreasing Giving-Up-Time with increasing density of non-infested host fruit or successive contact with pheromone-marked fruit.

The Mediterranean fruit fly, *Ceratitis capitata*, is one of the world's most economically important fruit fly pests, known to attack more than 200 species of fruit and vegetables. Several factors have been found to influence the degree of host fruit discovery and oviposition by medflies. These include the size, color, and chemical composition of the fruit, presence or absence of fruit marking pheromone, and the physiological state, genetic origin, and nature of prior experience of the female (Prokopy, 1983; Prokopy *et al.*, 1984; McDonald & McInnis, 1985; Carey *et al.*, 1986; Cooley *et al.*, 1986; Katsoyannos *et al.*, 1986; McDonald, 1986; Vita *et al.*, 1986). Only one study, however, has involved some assessment of the fruit foraging behavior of individual medfly females under non-laboratory conditions. Prokopy *et al.* (1986) found that mature medfly females released onto field-caged plants remained just as long and were just as likely to discover artificially-placed host fruit on certain non-host plants as on host plants.

Here, we examined quantitatively the foraging behavior of medfly females on field-caged host trees harboring varying densities of non-infested host fruit or host fruit that received marking pheromone.

Materials and methods

All medflies tested for behavioral response were wild, having originated from larvae that infested field-collected fruit of unsprayed loquats, *Eriobotryia japonicia* (Thunb.) Lindl., taken from the Kula area of the island of Maui in Hawaii. This population of medflies had access to a wide range of intermixed host and non-host plants (Wong *et al.*, 1983). Upon eclosion, females were held together with males in cages supplied with food (yeast hydrolysate and sucrose) and water (but no fruit) under laboratory conditions (25 °C, 80% r.h., 13 h natural daylength).

All tests were conducted in two cylindrical 3.5 × 3.5 × 3 m clear-nylon-screen field cages on the grounds of the USDA Tropical Fruit and Vegetable Research Laboratory in Honolulu. The top of the cage was covered with a partly opaque tarpaulin to exclude direct sunlight and rainfall. A single non-fruiting lemon tree, *Citrus limon* (L.) Burm. f. (a host of medfly), rooted in a pot was positioned 1 m above ground at the center of each cage. The tree exhibited the following characteristics: canopy diam = 84 or 81 cm; canopy height = 58 or 64 cm; total no. leaves = 138 or 139; mean surface area per leaf = ca. 58 cm^2 for each tree. Before being used in tests, the foliage and stems of each tree were rinsed gently but thoroughly with water to remove any adhering substances.

There were four treatments per tree: either 0, 3, or 12 non-infested kumquat fruit, *Fortunella japonica* (Thunb.) Swingle (a host of medly), or 12 kumquat fruit infested with medfly eggs and covered by medflies with marking pheromone deposited during ovipositor dragging on the fruit surface after egglaying (Prokopy *et al.*, 1978). Fruit densities (number of fruit relative to plant canopy volume) were chosen so as to be roughly comparable to those employed in studies on *R. pomonella* by Roitberg *et al.* (1982) and the Queensland fruit fly, *Dacus tryoni* (Froggatt), by B. Fletcher & Prokopy (unpub. data). Fruit which, during a trial, received one or more ovipositions (manifested via the dragging of the ovipositor following egg deposition (Prokopy *et al.*, 1978)) were replaced with fresh specimens of like type at the end of each treatment replicate. The kumquats (ca. 20 mm diam) were obtained from a local supermarket, rinsed thoroughly in water before use, hung by wire, and spaced evenly throughout the tree canopy. Each fruit received four evenly spaced punctures

with a dissecting needle to facilitate entry of the ovipositor into the flesh. Pheromone-marked, egg-infested kumquats were prepared by exposing them during the preceeding 18 h (3 PM – 9 AM) to 12 mature females of laboratory colony origin (colony was in continuous culture for more than 300 generations). A preliminary test confirmed the results of Prokopy *et al.* (1978) that wild medfly females assayed in lab cages refrained to an equal degree from attempting oviposition in fruit marked with pheromone by females of this laboratory colony and fruit marked by females of wild origin.

For testing, a single female (12 – 17 days old) was selected at random from a laboratory cage and allowed to oviposit in a kumquat fruit affixed to a dissecting probe and held within the tree canopy. Immediately following completion of marking pheromone deposition, the female was transferred gently onto a leaf at the lower center of the canopy. To ensure uniformity of procedure, flies were always released onto the same leaf. Using either a stopwatch and tape recorder or a TRS-80 portable computer, we monitored the location and duration of an array of fly behaviors until the fly flew from the tree (none crawled off) or 60 min elapsed (only six flies, all from the treatment with 12 non-infested fruit per tree, remained the full 60 min). We also measured ambient temperature at the base of the tree canopy. Because fewer than 1% of all females tested exhibited any feeding behavior during the assay period, we excluded time spent feeding from data analysis. In Roitberg *et al.* (1982), one of the *R. pomonella* behaviors assessed was 'search time', which consisted of time spent moving (one or more body lengths/sec exclusive of ovipositor dragging on fruit following egglaying) plus time spent scanning the environment through periodic side-to-side head movements while the body was otherwise stationary. Because we did not feel confident in assessing accurately the head movement behavior of medflies, we partitioned fly behavior simply according to time moving as defined above (= a component of time searching) and time resting (inclusive of time grooming).

Each fly was tested only once, following which it was immediately offered a kumquat. Those females that failed to attempt oviposition into such fruit after testing on a tree were considered as having been in a physiological state non-conducive to oviposition site foraging and were excluded from data analysis (= ca. 2% of all individuals tested). To minimize experimental error, we alternated treatments in a systematic fashion.

For comparing treatment median values, we used a median test (Siegel, 1956) at the 0.05 level. For comparing proportions of treatment females exhibiting a response, we used a G-test at the 0.05 level (Sokal & Rohlf, 1981).

Results

Medflies foraging in trees harboring non-infested fruit tended to spend more total time, more time moving, and more time resting on a tree as fruit density increased (Table 1). Conversely, Giving-Up-Time (GUT) tended to decrease as fruit density increased (GUT equals time since the last oviposition – either in the fruit from which the fly was initially released or in a fruit encountered while foraging – until departure from the tree). There was no consistent pattern among the three fruit density levels in number of leaves visited and total time, time moving, or time resting on foliage. On the other hand, flies on trees with 12 fruit spent significantly more total time on fruit, visited significantly more fruit, and attempted oviposition a significantly greater number of times than flies on trees with three fruit. On a per-fruit-visit basis, however, there were no significant differences between these two treatments in total time on fruit, time ovipositing or dragging the ovipositor, or time since completion of ovipositor dragging until departure from a fruit. While a significantly smaller proportion of females discovered fruit at the 3- than at the 12-density level, a significantly greater proportion of total visits at the 3-density level resulted in an oviposition attempt and ovipositor dragging (Table 2). For both of these density levels of non-infested fruit, the proportion of first visits to a fruit that culminated in an oviposition attempt or ovipositor dragging bout was much greater than that for subsequent visits to the same fruit.

Medflies on trees with 12 infested (pheromone-marked) fruit spent significantly less total time and less time resting on a tree but exhibited a significant-

Table 1. Comparison of *C. capitata* behavior on host trees harboring varying densities or qualities of kumquat fruit (N = 24 flies/treatment; median values are given)[a].

Parameter	0 fruit	3 non-infested fruit	12 non-infested fruit	12 infested fruit
Entire tree				
Total time (s)	220c	987ab	1497a	600b
Time moving	33b	112a	268a	197a
Time resting	126c	286ab	422a	221bc
GUT	220ab	167ab	135b	240a
Foliage				
No. leaves visited	3a	4a	5a	4a
Total time	221a	223a	208a	144a
Time moving	35a	42a	44a	38a
Time resting	119a	157a	136a	123a
Fruit				
No. fruit visited	–	1b	4a	5a
No. oviposition attempts	–	5bc	10a	1c
No. ovipositor draggings	–	2a	3a	0b
Total time[b]	–	663b	1353a	300b
Total time/fruit visit[c]	–	1061a	1353a	359b
Time moving/fruit visit[c]	–	69a	31b	34b
Time resting/fruit visit[c]	–	148a	61b	14c
Time ovipositing/attempt	–	53a	47a	20b
Time dragging/bout	–	70a	66a	38b
Time from end of dragging to departure from that fruit	–	56a	49a	44a

[a] Values followed by same letter within row not significantly different at 0.05 level.

[b] Median values based on all females tested, including those which did not visit any fruit.

[c] Median values based on only those females which visited a fruit.

ly longer GUT than flies on trees with 12 non-infested fruit (Table 1). There were no significant differences between these two treatments in total time, time moving, or time resting on foliage, or in number of leaves or fruit visited. But flies on trees with 12 pheromone-marked fruit attempted oviposition and engaged in ovipositor dragging a significantly fewer number of times than flies on trees with 12 non-infested fruit and spent significantly less total time on fruit, less total time and less time resting per fruit visit, less time ovipositing per attempt, and less time dragging the ovipositor per dragging bout. There was no difference between these two treatments in time since completion of ovipositor dragging until departure from a fruit. Nor was there any difference in proportion of females discovering fruit

(Table 2). However, a significantly smaller proportion of total visits to pheromone-marked fruit resulted in an oviposition attempt or ovipositor dragging bout than visits to non-infested fruit. These latter two differences between treatments are considerably accentuated if one considers only the very first visit to a given fruit (omitting succeeding visits to the same fruit).

Regression analyses of the performances of various behaviors in each treatment in relation to ambient temperature reveal, with a single exception, no significant influence of temperature on total time moving or resting on a tree, GUT, or total number of leaves or fruit visited (Table 3). The single exception was a significant negative relation between temperature and time resting in trees devoid of fruit.

Table 2. Comparison of *C. capitata* behavior on host trees harboring varying densities or qualities of kumquat fruit (% values given)[a].

Parameter	3 non-infested fruit		12 non-infested fruit		12 infested fruit	
	N	%	N	%	N	%
Flies discovering a fruit	24	67b	24	96a	24	88ab
Oviposition attempts						
Total visits to fruit resulting in oviposition attempt	32	72a	129	47b	153	27c
First visit to fruit resulting in oviposition attempt	22	91a	71	76a	77	32b
Self-marked fruit receiving oviposition attempt on re-visits	8	25a	41	17a	11	18a
Non-self-marked fruit receiving oviposition attempt on re-visits	2	50a	17	29a	65	23a
Ovipositor dragging						
Total visits to fruit resulting in ovipositor dragging	32	66a	129	36b	153	8c
First visits to fruit resulting in ovipositor dragging	22	82a	71	55b	77	10c
Self-marked fruit receiving ovipositor dragging on re-visit	8	25a	41	10a	11	9a
Non-self-marked fruit receiving ovipositor dragging on re-visit	2	50a	17	18a	65	6a

[a] See Table 1.

Table 3. Correlation between *C. capitata* behavior in host trees and ambient temperature (°C) (r^2 values given).

Parameter	0 fruit	3 non-infested fruit	12 non-infested fruit	12 infested fruit
Time moving in tree	0.08	0.01	0.01	0.01
Time resting in tree	0.18*	0.07	0.00	0.01
GUT	0.15	0.02	0.00	0.00
No. leaves visited	0.06	0.00	0.01	0.01
No. fruit visited	–	0.00	0.09	0.01

* Significant correlation at 0.05 level.

Discussion

The nature of the intra-tree host fruit foraging behavior of medflies under the varying fruit density and quality conditions tested here proved remarkably similar, in nearly all aspects measured, to that of *R. pomonella* in earlier studies. Thus, medflies (a) emigrated within a few minutes after release onto small host trees devoid of fruit; (b) visited more fruit, oviposited more often, and remained longer on host trees that harbored higher densities of non-infested fruit than lower densities of non-infested fruit; (c) accepted a proportionately smaller number of fruit visited as density of non-infested host fruit increased; and (d) exhibited a decreasing GUT with increasing density of non-infested host fruit.

256

The trends observed here in medflies toward increasing time (energy) investment in a patch with increasing richness of resource items and toward proportionately lower acceptance of resource items at higher levels of abundance (sometimes expressed as greater 'selectivity' among resource items – e.g. Roitberg et al. (1982)) are consistent with foraging behavior theory (Hassel & Southwood, 1978; Pyke, 1984) and have been observed in butterflies (Rausher, 1983) and several parasitoid insects (e.g. van Alphen & Galis, 1983; Cloutier, 1984). There exists conflicting theoretical opinion (e.g. Charnov, 1976; McNair, 1982) and conflicting evidence (e.g. Krebs et al., 1974; van Lenteren & Bakker, 1978; van Alphen & Galis, 1983) as to whether GUT in a patch should decrease, stay the same, or increase with increasing resource density or quality. The trend in medflies toward decreasing GUT with increasing host density may simply reflect depleted egg load (and hence a diminished propensity to search for additional fruit) at high fruit density. Alternatively, as suggested for R. pomonella by Roitberg et al. (1982), the trend could stem from the fact that, at higher fruit density, most flies would discover new fruit much sooner than they would at lower fruit density. Thus, most flies that would leave a tree before discovering new fruit at high fruit density would do so within a comparatively short period of time. Otherwise, they would discover a fruit. Further research is required to establish whether medflies do in fact determine resource patch departure on the basis of GUT or via some other 'rule' or combination of rules (Pyke, 1984).

Bell (1985), in providing an elegant, more mechanistic analysis of GUT than heretofore, proposes that GUT in a resource patch is related to transition from local searching (manifest as a relatively high turning rate and low locomotory rate) to ranging (manifest as a relatively low turning rate and high locomotory rate). Our observations concur with Bell's model. Thus, in the medfly, during the early stages of intra-tree foraging, females characteristically engaged only in occasional relatively short, straight-line flights (ca. 5 s or less) among leaves and fruit. Toward the terminus of intra-tree foraging, flights were more frequent and tended to be of a longer-distance, looping type and of much longer duration (up to ca. 15 s). We have observed a similar pattern in R. pomonella, except that average duration of nearly all individual intra-tree flights tends to be far less (no more than 3 – 4 s) than in the medfly.

Of interest is the fact that for each treatment, the proportion of initial visits of medflies to an individual fruit that culminated in an oviposition attempt was considerably greater than that for subsequent visits to the same fruit (Table 2). This was true irrespective of whether marking pheromone had been deposited on the first visit or not, although there was a tendency in each treatment toward greater rejection of fruit self-marked with pheromone than fruit non self-marked. A similar phenomenon has been observed in R. pomonella (B. D. Roitberg & Prokopy, unpub. data) and certain parasitoids (van Alphen & Galis, 1983). Why, even in the case of non-pheromone-marked, non-infested fruit, such a comparatively low proportion of fruit should have been accepted for oviposition during revisits is uncertain, but could have been due to declining propensity to oviposit with decreasing egg load or to recognition of an already-visited fruit on the basis of its location or its peculiar chemical or physical properties.

As was found for R. pomonella (Roitberg & Prokopy, 1984), variation in temperature at which assays of medflies were carried out explained only a very minor part of the variation in foraging behavior among flies within treatments. Temperature is known to affect foraging velocity in other insects (e.g. Rissing, 1982). The apparent lack of an appreciable effect in this study could have been due to (a) lack of sufficient breadth (especially at the lower end of the scale) in the range of temperatures at which flies were assayed (25 – 36 °C); or (b) the influence of temperature having been overridden by the influence of vapor pressure deficit or wind velocity (neither of which we measured).

What are the pest management implications of our findings? First the fact that fruit-foraging medflies emigrate very rapidly from trees devoid of host fruit suggests that fruit stripping, while of positive value in removing larval-infested fruit, could have counter-productive effects. Thus, unless the flies were killed by pesticide application or some other method *before* fruit were stripped from the tree, the

flies might contribute to rapid expansion of the region of infestation by moving to fruiting host trees outside the perimeter of the eradication zone. Second, if medfly fruit marking pheromone could be chemically identified, as has been accomplished by Hurter *et al.* (1987) with the marking pheromone of *R. cerasi* L., our findings suggest that the synthetic equivalent, sprayed onto host trees, could elicit comparatively rapid departure of medflies from treated trees and afford significant protection against medfly oviposition, provided traps were used on nearby trees to capture emigrating females.

Résumé

Relations entre la densité et la qualité des fruits et le comportement de prospection de Ceratitis capita-ta *à l'intérieur d'un arbre*

Nous avons étudié le comportement de prospection dans un arbre, de femelles d'une population sauvage de *C. capitata*, libérées individuellement à l'intérieur de cages contenant des *Eriobotrya japonica* (kumquat), portant chacun 3 densités différentes de fruits no contaminés (0, 3, 12 par arbre) et chacun 2 niveaux de qualité de fruits: 12 fruits non infestés ou 12 fruits contaminés par des oeufs et recouverts de phéromone de marquage de l'hôte. *C. capitata* avait terndance à rester plus longtemps dans les arbres, à visiter plus de fruits avant le quitter, à pondre plus souvent, à accepter proportionnellement un nombre plus réduit de fruits déjà visités, à émigrer plus tôt après la ponte du dernier oeuf (c'est-à-dire à présenter un temps d'abandon plus bref), quand la densité des fruits non contaminés augmentait. *C. capitata* a dépensé beaucoup moins de temps, pondu beaucoup moins souvent, et présenté un temps d'abandon plus long sur les arbres portant des fruits marqués par la phéromone que sur ceux ayant des fruits non contaminés. Les variations de température dans la gamme de cells où les observations ont eu lieu (23 – 36 °C) n'ont eu qu'une faible influence décelable sur le comportement de prospection. Nous avons comparé nos résultats avec ceux publiés sur la prospection à l'intérieur de l'arbre par une autre téphriti-de (*Rhagoletis pomonella*) et avec la théorie dominante sur le comportement de prospection. Nous discutons les conséquences de nos résultats sur les stratégies de lutte contre *C. capitata*, en particulier l'élimination des fruits dans les plans d'erradication et l'utilisation de phéromone synthétique de marquage.

Acknowledgements

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